Bacular Measurements for Age Determination and Growth in the Male South African Fur Seal, *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae)

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Morphology, relative size and growth of the baculum in 103 South African fur seals, *Arctocephalus pusillus pusillus,* from the Eastern Cape coast of South Africa are described. Bacular measurements (n = 8 linear variables and mass) were examined in relation to standard body length (**SBL**), bacular length (**BL**) and chronological age (y) using linear regression. Animals ranged from < 1 month to ≥ 12 y. Bacular shape was most similar to *Callorhinus ursinus (*Northern fur seal) and *Zalophus californianus* (California sea lion). For the range of ages represented in this study, the baculum continued to increase in size until at least 10 y; with growth slowing between 8-10 y, when social maturity (full reproductive capacity) is attained. Growth in bacular length (**BL**), distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width, distal width and proximal shaft height peaked at 10 y. In the largest animal (age ≥ 12 y), maximum bacular length was 139 mm and mass 12.5 g. Relative to **SBL**, bacular length (**BL**) increased rapidly in young animals, peaked at 9 y (6.9%), and then declined. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length. At 9 y, mean bacular length and mass was 117 ± 2.7 (± SE, n = 4) mm and 7 ± 0.7 (4) g; growth rates in bacular length and mass were 311% and 7125% (relative to age zero), and 5% and 27% (between years); and bacular length (**BL**) was about 6.9% of **SBL**. For all males ≥12 months, most bacular variables grew at a faster rate than **SBL** and **BL**. Exceptions included proximal width which was isometric to **SBL**; distal width and distal shaft height which were isometric to bacular length; and proximal width which was negatively allometric relative to **BL**. Bacular length (**BL**) was found to be a useful predictor of **SBL** and seal age group (pup, yearling, subadult, adult), but only a 'rough indicator' of absolute age.

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KEYWORDS: age classification, age determination, *Arctocephalus pusillus pusillus*, baculum morphometrics, Otariidae, Pinnipeds, South African fur seal, standard body length.

INTRODUCTION

The mammalian baculum (*os penis*) is found in all carnivores, except the hyena (Ewer, 1973). This morphologically diverse bone has received considerable scientific attention in the field of mammalian systematics (McLaren, 1960; Sutton and Nadler, 1974; Kim et al., 1975; Morejohn, 1975; Lee and Schmidly, 1977; Patterson and Thaeler, 1982; Patterson, 1983), and has been used as an index of age, puberty and social maturity for several species of mammals, including pinnipeds (Hamilton, 1939; Elder, 1951; Laws, 1956; Hewer, 1964; Bester, 1990). The function of the baculum in carnivorous mammals remains controversial. It may lack specific function (Burt, 1939; Mayr, 1963) or may be adaptive in various interactions of males and females during copulation, with function differing considerably between species (Scheffer and Kenyon, 1963; Long and Frank, 1968; Ewer, 1973; Miller, 1974; Morejohn, 1975; Patterson and Thaeler, 1982; Eberhard, 1985, 1996; Dixson, 1995; Miller et al., 1996, 1998, 1999; Miller and Burton 2001). The baculum bone of carnivores is classified as a heterotopic bone because it forms from ossification of connective tissue (Miller, 2009). The proximal end of the baculum is attached to the fibrous *corpora cavenosa penis*.

Within the Otariidae, information on the morphology of the baculum is available for *Arctocephalus pusillus pusillus* (South African fur seal), *Arctocephalus pusillus doriferus* (Australian fur seal); *Arctocephalus gazella* (Antarctic fur seal); *Arctocephalus tropicalis (*Sub Antarctic fur seal); *Callorhinus ursinus (*Northern fur seal); *Eumetopias jubatus* (Stellers sea lion); *Neophoca cinerea*, *(*Australian sea lion); *Otaria byroni* (South American fur seal); *Phocarctos hookeri* (New Zealand or Hookers sea lion) and *Zalophus californianus* (California sea lion) (Chaine, 1925; Hamilton, 1939; Rand, 1949,1956; Scheffer, 1950; Mohr, 1963; Scheffer and Kenyon, 1963; Kim et al., 1975; Morejohn, 1975; Bester, 1990; Laws and Sinha, 1993). Of these, the northern fur seal has been studied in most detail (Scheffer, 1950; Scheffer and Kenyon, 1963; Kim et al., 1975; Morejohn, 1975).

Information on bacular growth based on bulls reliably aged from tooth structure, or on bulls of known age (i.e. bulls tagged or branded as pups), is only available for *Callorhinus ursinus* (northern fur seal) (Scheffer, 1950), *Arctocephalus tropicalis* (Sub Antarctic fur seal) (Bester, 1990) and *Arctocephalus pusillus pusillus,* South African fur seal (Oosthuizen and Miller, 2000). A large data set of reliably aged material is also available on the baculum of the phocid harp seal (*Pagophilus greonlandicus*) (Miller et al., 1998; 1999; Miller and Burton 2001). These studies indicate that: (i) the baculum increases in length and mass with increasing age; (ii) bacular growth may be fairly constant, as in the northern fur seal, harp seal and subantarctic fur seal, or there may be an increase in the rate of growth at puberty, as has been suggested in the South African fur seal; (iii) there may be a sudden increase in the rate of bacular growth when individuals attain social maturity (full reproductive capacity); and (iv) there is a decline in the rate of bacular growth in socially mature bulls.

Seal baculum and testicles are used in oriental aphrodisiac medicine and gastronomy and so there is a legal and illicit trade in seal genitalia (Miller, 2009). Demand outstrips supply and the origin of material sold is often in doubt. Bacula from South African fur seals are part of the legal trade in seal body parts. Other southern fur seals are not legally hunted for body parts. It would be naïve to imagine that there is not some illicit trade in body parts from other southern hemisphere seals and sea lions. The other major legal source of seal body parts is from the Harp seal (*Pagophilis greonlandicus*) where illustrations, information on morphometrics, growth and development of the baculum are available (Miller and Burton, 2001; Miller 2009). Museums and zoologists can be asked to identify seal body parts by customs authorities to determine whether they are from legally hunted species or not: morphometric knowledge of the seal baculum is important for conservation reasons.

Here we examine the bacula of 103 male South African fur seals from the Eastern Cape coast of South Africa. We provide illustrations of bacula from the species to aid in identification. Specific objectives were to: (i) describe the general morphology of the baculum; (ii) quantify growth of bacular measurements (n = 8 linear variables and mass) relative to standard body length (**SBL**) (n = 89 bulls), bacular length (**BL**) (n = 103 bulls), and chronological age (n = 50 bulls); (iii) determine if the baculum is a useful indicator of social maturity; and (iv) determine if bacular length (**BL**) is a useful indicator of age and/or standard body length (**SBL**). Currently there are only two reliable means of determining the age of South African fur seals (Stewardson, 2001; Stewardson et al., 2008). The first is based on tagging as pups, the other is based on dentition but the dentition method is only valid for bulls less than about 12 y. Unfortunately, age assignment based upon skull suture closure criteria are known to be inaccurate and of value only for seals ≥ 12y in South African fur seals (Stewardson, 2001) which invalidates some early work on baculum statistics vs. age (Rand, 1956; Mohr, 1963).

MATERIALS AND METHODS

Collection of specimens

South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM), Port Elizabeth, South Africa. One animal (PEM2238) was collected NE of the study area, at Durban. From this collection, bacula from 103 males were selected for examination. The list of specimens used in the present study, along with their

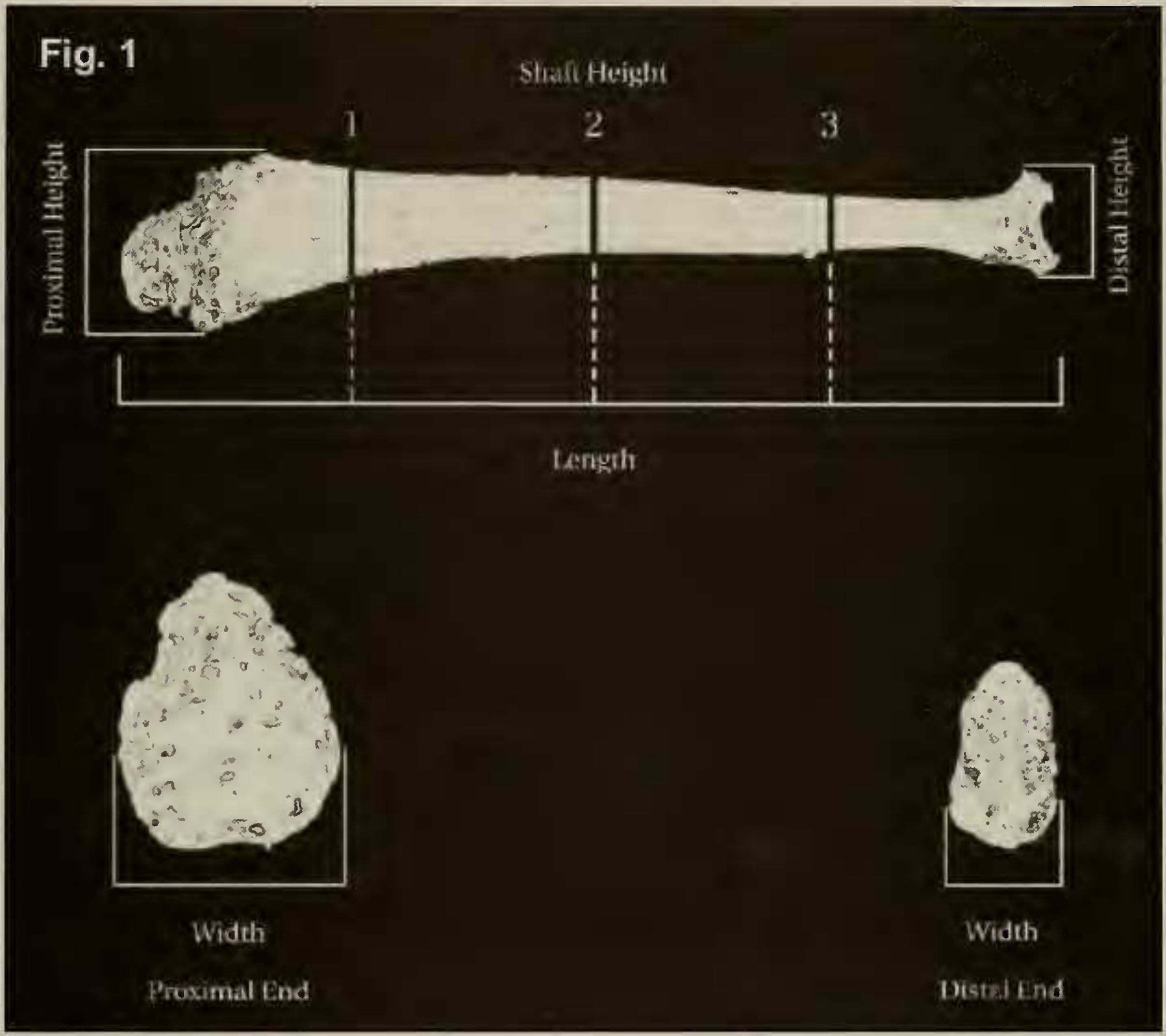

Fig. 1 Diagram of a South African fur seal baculum indicating the variables measured (Var 1-8): Bacular length (Var 1 or BL); Proximal height (Var 2); Proximal width (Var 3); Distal height (Var 4); Distal width (Var 5); Three cross sectional parameters of the shaft: (1) Proximal shaft height (Var 6); (2) Middle shaft height (Var 7) and (3) distal shaft height (Var 8). Specimen provided by P Shaughnessy.

museum ascension numbers and location and dates of collection, are listed in Stewardson et al. (2008). Apart from specimens collected before May 1992 (n = 29), all specimens were collected by the first author and were found dead, dying or had drowned in fishnets.

Preparation and measurement of bacula

Bacula were defleshed and macerated in water for 1-2 months. Water was changed regularly. Bacula were then washed in mild detergent and air dried at room temperature. Dry specimens were weighed using an electronic balance and measurements (n = 8 linear variables) were taken using a vernier calliper (to 0.1 g and 0.1 mm) following Morejohn (1975) (Fig. 1). All bacular measurements were recorded by the first author.

Age determination

Of the 103 bulls in the study: (i) 40 were aged from counts of incremental lines observed in the dentine of upper canines (growth layer groups, GLG) as described in Stewardson et al. (2008). Dentition-based ages fell into 3 categories: (i) age range 1-10 y; (ii) 10 were identified as adults > 12 y (i.e., pulp cavity of the upper canine was closed); and (iii) 53 for a variety of reasons could not be aged. None were tagged individuals. South African fur seals older than 12 y cannot be aged from counts of growth layer groups (GLG) in the dentine of upper canines because the pulp cavity closes (Stewardson et al., 2008).

In studies of South African fur seals, 1st November is taken as the birthdate of all seals based upon estimates of the average birthdate of pups in breeding

Table 1. The age distribution of male South African fur seals used in the present study. Estimated age from counts of incremental lines observed in the dentine of upper canine (n = 40). An additional 10 males were ≥ 12 y, i.e., pulp cavity closed. Pups were greater than one month of age.

Age group	Age (y)	Frequency	Percentage
Pups	< 1	3	6
Yearling	1	5	10
Subadult	2	0	0
	3	0	0
	4	1	2
	5	3	6
	6	2	4
	7	11	22
Adult	8	8	16
	9	4	8
	10	3	6
	≥ 12	10	20
Total		50	100

colonies (Rand, 1949; Oosthuizen and Miller, 2000). For this study, the following age groups were used: pup (< 1 months to 6 months); yearling (7 months to 1 y 6 months); subadult (1 y 7 months to 7 y 6 months); and adult (> 7 y 7 months) (rounded to whole years in Table 1) (see Stewardson et al., 2008, 2009). No individuals of 2 y to 3 y were available. Data on very old bulls that had been tagged as pups were not available. The estimated longevity of bull South African fur seals is about 20 y based primarily on zoo animals (Wickens, 1993). Currently, examination of tooth structure is the most precise method of age determination in untagged pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997) and Stewardson et al. (2008).

The limitations of age determinations based upon dentition become apparent if one realises that it would be reasonable to assume that the longevity of South African fur seal bulls in the wild would be at least 15 y (based upon documentation on the Australian fur seal, *A. pusillus doriferus*; Arnould and Warneke, 2002), which implies that dentition can only age male South African fur seals up to only about 2/3 of their total potential lifespan.

Statistical analysis

Bacular measurement error

Duplicate measurements of bacular length were taken from 50 randomly selected bacula to assess measurement error. The Wilcoxon sign-rank test was used on the differences to test H_0: median = 0, versus H_1: median ≠ 0.

Bacular length (BL) expressed in relation to standard body length (SBL)

Standard body length (**SBL**) is defined as the length from the nose to the tail in a straight line with the animal on its back (Committee on Marine mammals, 1967). Growth in **BL**, relative to standard body length (**SBL**), was calculated as follows, using paired samples only:

BL (mm) /SBL (mm) x 100%

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Bacular growth relative to age zero, RGR Y_0

Percent change in bacular measurement at age t, relative to value at age zero, was calculated as follows:

$$[(Y_t - Y_0)/Y_0] \times 100\%$$

where, Y_0 = mean bacular measurement from pups < 1 months of age (age zero), and Y_t = mean bacular measurement for age t (age class in y).

Bacular growth relative to the previous year (annual bacular growth), RGR Y_{t-1}

The percent change in value at age t, relative to the value at age t-1, was calculated as follows:

$$[(Y_t - Y_{t-1})/Y_{t-1}] \times 100\%$$

where, Y_t = mean bacular measurement for age (t), and Y_{t-1} = mean bacular measurement for age t-1 (between years). RGRs were calculated for bulls that were 7-10 y.

Bacular length (BL) as an indicator of SBL and age

The degree of linear relationship between Log_e (**BL**), Log_e (**SBL**) and Age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (pup, yearling, subadult, adult) using one independent variable, bacular length (see Stewardson et al., 2008, 2009 for further details).

Bivariate allometric regression

The relationship between each bacular measurement (**Var 1** to **9**) and: (i) **SBL**, (ii) **BL**, and (iii) age (y), was investigated using linear regression, semi-log plots (Log_e y = mx + b) or the log/log logarithmic transformation of the allometric equation, $y = ax^b$, which may equivalently be written as $Log_e\ y = Log_e\ a + b.Log_e\ x$. For most analyses the three one month-old pups were not included (hence n = 37). 'Robust' regression (Huber M-Regression) was used to fit straight lines to the untransformed or transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons and Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson et al. (2008).

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and SPLUS 7.0 (MathSoft, Inc., Seattle, 2005, version 7.0).

RESULTS

Bacular measurement error

Of the 50 bacula that were measured twice, measurements were reproducible at the 5% significance level (p-value = 0.052).

Bacular morphology

Bacular length (**BL**) and mass ranged from 26.6 to 139.3 mm and 0.1 to 12.5 g, respectively (Table 2).

The youngest animals in the sample were < 1 month of age. In these individuals, the baculum was short, thin and rod-like, with no obvious distinction between the proximal and distal ends (Fig. 2a and 2b). The shaft was slightly curved anteriorly (variable).

In yearlings, the baculum increased substantially in length and mass (Table 3). The distal end was slightly rounded but, there was no sign of bifurcation (Fig. 2c).

In subadults, most bacula curved upwards at the distal end (i.e., superiorly, see Fig. 2d). At the distal end of the baculum, there were two narrow projections (knobs): a well-developed ventral knob and a less prominent dorsal knob (Fig. 2d). In older subadults, the ventral knob extended upwards and outwards forming a double knob (variable). The proximal end of the bacula was bulbous in all bulls ≥ 4 y.

In adults (> 8 to 9 y) the baculum was well developed, with pronounced thickening of the proximal end. Contrast Fig. 2d which is a 7 year old subadult with Fig. 2e which is a 10 year old (Fig. 2). At the bifurcated distal end, the ventral knob usually extended further than the dorsal knob. In older males, the baculum was more robust, but not necessarily longer. Small osseous growths were commonly found on the proximal end of the baculum (n = 18 subadult and adult bacula) creating a rough surface where the fibrous tissue of the *corpus cavernosum penis* attached. In some older specimens (n = 16 bacula), small knob-like growths (usually 1 or 2) were observed along the edge of the urethral groove, at the proximal ventral surface of the baculum.

Bacular length expressed in relation to SBL

Relative to **SBL**, **BL** increased rapidly in young animals, peaks at about 9 y (6.9%), and then declines in old bulls ≥ 12 y, i.e., adults 8 to 10 y, mean 6.6 ± 0.122% (n = 13) vs. adults ≥ 12y, 6.09 ± 0.32% (n = 9); t-test p< 0.01. More detailed relative growth patterns for subadults, adults and old bulls could not be established because the sample size is too small and **SBL** was not available for all specimens (**SBL**s for 12 animals drowned in fishnets were not recorded because rough conditions at sea precluded measurement of **SBL**).

Bacular growth relative to age zero, RGR Y_0

Percent change in value of bacular measurement at age *t*, relative to value at age zero, is presented in Table 4. In yearlings, bacular mass was the most rapidly growing variable, followed by bacular length, proximal height, distal height, proximal shaft height, proximal width and distal shaft height/middle shaft height. Distal width showed little sign of growth.

Growth of bacular variables continued to increase until at least 10 y, with bacular mass, middle shaft height and distal shaft height expressing continued growth in bulls ≥ 12 y. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length (Table 4).

Bacular growth relative to the previous year, RGR Y_{t-1}

Percent change in value of bacular measurement at age *t*, relative to value at age *t*-1, for bulls 7-10 y, is presented in Table 4. Percent increment in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width distal width and proximal shaft height peaked at 10y.

Age group	Age (y)	n	Var 1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	28.5 ± 1.6	2.6 ± 0.5	3.5 ± 0.3	2.2 ± 0.3	1.7 ± 0.2	2.4 ± 0.2	2.2 ± 0.2	1.9 ± 0.1	0.1 ± 0.0
			(9.6)-	(31.5) 9.0%	(12.5) 12.3%	(24.7) 7.8%	(18.3) 5.9%	(13.6) 8.3%	(15.7) 7.7%	(7.9) 6.8%	(0) 0.4%
Yearling	1	5	47.8 ± 1.7	3.5 ± 0.1	4.2 ± 0.1	2.9 ± 0.2	1.7 ± 0.04	3.0 ± 0.1	2.5 ± 0.1	2.2 ± 0.2	0.3 ± 0.03
			(8.0) -	(7.7) 7.3%	(6.6) 8.8%	(15.8) 6.1%	(5.9) 3.6%	(5.0) 6.2%	(12.2) 5.2%	(18.2) 4.6%	(23.6) 0.6%
Subadult	4	1	86.6	5.3	6.6	7.3	2.8	5.9	5.5	4.4	2.4
	5	3	97.1 ± 4.6	9.4 ± 2.5	7.7 ± 0.9	9.4 ± 0.6	4.2 ± 0.8	7.0 ± 0.6	5.8 ± 0.2	5.0 ± 0.2	3.4 ± 0.4
			(8.2)-	(45.3) 9.7%	(20.9) 7.9%	(10.5) 9.7%	(31.0) 4.3%	(13.6) 7.2%	(4.6) 6.0%	(8.4) 5.1%	(21.2) 3.5%
	6	2	99.5 ± 2.8	8.2 ± 0.1	6.7 ± 1.5	10.9 ± 0.1	3.9 ± 0.6	7.1 ± 0.9	5.4 ± 0.2	4.5 ± 0.1	3.1 ± 0.1
			(3.9)-	(0.9) 8.2%	(31.7) 6.7%	(0.7) 10.9%	(20.2) 3.9%	(17.9) 7.1%	(5.2) 5.4%	(3.1) 4.5%	(2.3) 3.1%
	7	11	101.4 ± 2.7	9.8 ± 1.0	7.6 ± 0.4	10.7 ± 0.6	4.0 ± 0.2	7.2 ± 0.3	6.3 ± 0.3	5.3 ± 0.2	4.1 ± 0.4
			(9.0) -	(33.4) 9.7%	(16.3) 7.5%	(17.8) 10.5%	(17.5) 4.0%	(14.8) 7.1%	(13.3) 6.2%	(14.3) 5.3%	(34.0) 4.0%
	4-7	**1 7**	**99.5 ± 2.1**	**9.3 ± 0.8**	**7.5 ± 0.3**	**10.3 ± 0.4**	**4.0 ± 0.2**	**7.1 ± 0.2**	**6.1 ± 0.2**	**5.1 ± 0.2**	**3.7 ± 0.3**
			(8.7) -	(34.6) 9.3%	(17.5) 7.5%	(17.5) 10.3%	(20.5) 4.0%	(14.4) 7.1%	(12.5) 6.1%	(13.9) 5.1%	(33.1) 3.7%
Adult	8	8	111.4 ± 3.1	11.3 ± 0.8	9.4 ± 0.6	12.2 ± 0.5	4.3 ± 0.1	8.0 ± 0.3	6.9 ± 0.2	5.6 ± 0.2	5.7 ± 0.5
			(7.8) -	(19.0) 10.8%	(18.5) 8.4%	(12.3) 11.0%	(9.5) 3.9%	(11.1) 7.2%	(8.7) 6.1%	(8.4) 5.0%	(23.9) 5.1%
	9	4	116.9 ± 2.7	10.4 ± 1.8	10.8 ± 1.6	12.4 ± 0.9	4.9 ± 0.7	8.1 ± 0.5	7.6 ± 0.3	6.3 ± 0.2	7.2 ± 0.7
			(4.6) -	(35.5) 8.9%	(29.3) 9.2%	(14.5) 10.6%	(29.2) 4.2%	(12.8) 7.0%	(7.9) 6.5%	(7.8) 5.4%	(18.4) 6.2%
	10	3	117.8 ± 2.9	14.0 ± 0.8	13.5 ± 1.9	13.2 ± 0.5	6.1 ± 0.4	10.6 ± 0.3	8.1 ± 0.4	6.5 ± 0.2	7.6 ± 0.6
			(4.3) -	(9.7) 11.9%	(24.5) 11.4%	(6.2) 11.2%	(12.5) 5.2%	(4.8) 9.0%	(8.1) 6.9%	(4.7) 5.5%	(14.1) 6.5%
	8-10	**15**	**114.2 ± 2.0**	**11.6 ± 0.7**	**10.6 ± 0.7**	**12.5 ± 0.4**	**4.8 ± 0.3**	**8.6 ± 0.3**	**7.3 ± 0.2**	**6.0 ± 0.1**	**6.5 ± 0.4**
			(6.6) -	(23.1) 10.2%	(26.4) 9.3%	(11.5) 10.9%	(22.0) 4.2%	(15.4) 7.5%	(10.6) 6.4%	(9.6) 5.2%	(23.2) 6.7%
	≥ 12	10	113.1 ± 3.8	11.4 ± 0.8	10.1 ± 0.7	13.3 ± 0.7	4.9 ± 0.5	10.0 ± 0.5 [8]	8.6 ± 0.6	6.6 ± 0.3	8.3 ± 0.9
			(10.7)-	(22.6) 10.1%	(20.9) 8.9%	(17.3) 11.7%	(28.4) 4.5%	(17.2) 8.8%	(23.6) 7.6%	(12.5) 5.8%	(34.2) 7.3%
Total		**50**	**50**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**
Mean for males ≥ 200 cm (n = 7)			127.7 ± 2.8	13.1 ± 0.3	9.9 ± 1.0	14.4 ± 0.4	5.0 ± 0.3	10.5 ± 0.5	9.2 ± 0.3	7.1 ± 0.3	10.9 ± 0.5
[Maximum value in brackets]			[139.3]	[14.0]	[13.7]	[15.7]	[5.8]	[12.2]	[10.2]	[8.1]	[12.5]

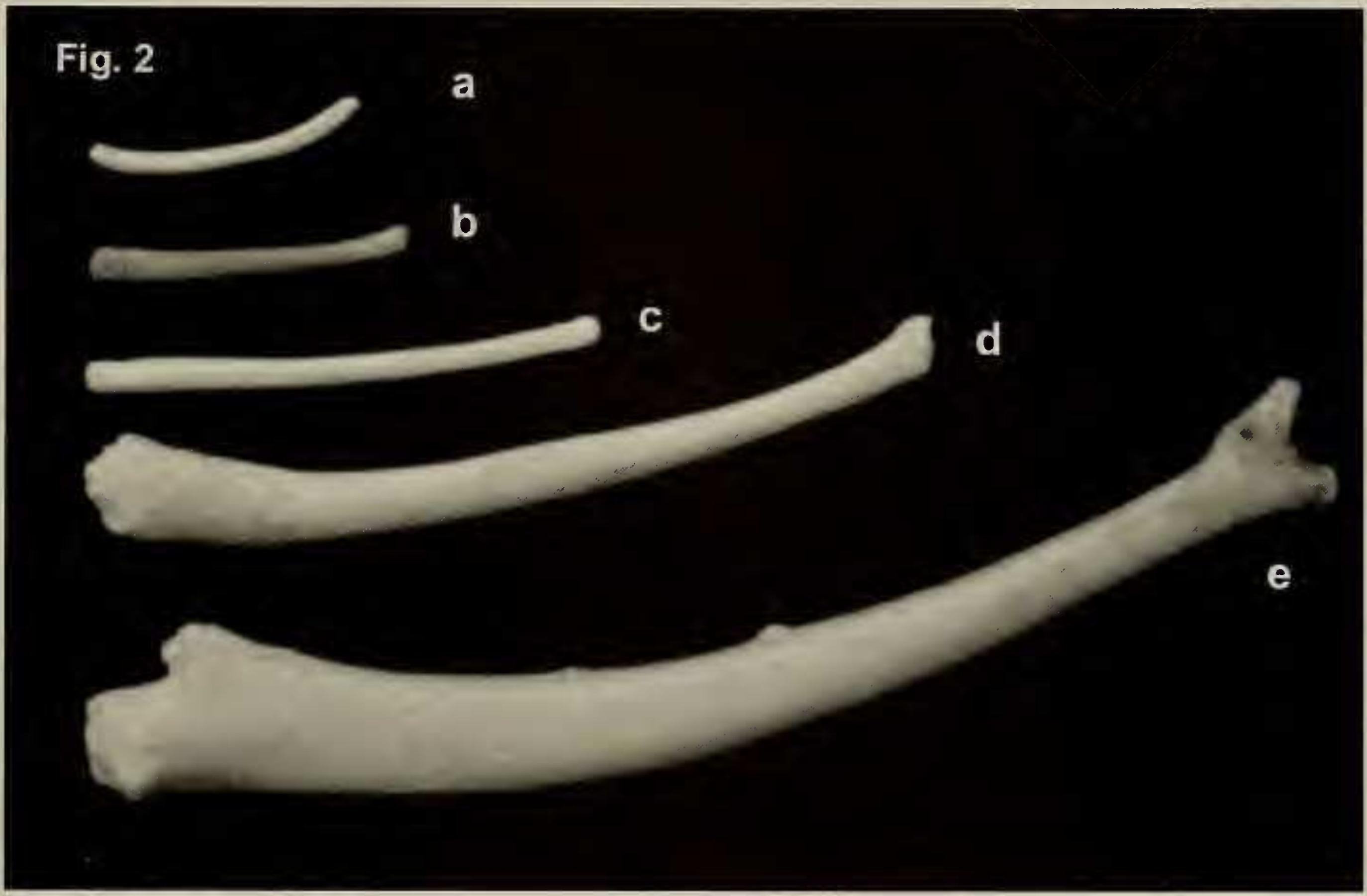

Fig. 2 Size and shape of the South African fur seal baculum in relation to age group: a. pup (PEM2020, 26.6 mm); b. pup (PEM2024, 31.6 mm); c. yearling (PEM2191, 50.7 mm); d. sub-adult, 7-y-old (PEM2053, 93.3 mm) and e. adult, 10-y-old (PEM2087, 123.3 mm).

Bacular length as an indicator of age

The plot of Bacular length (BL) vs. Age (y) is shown in Fig. 3. For animals 1-10 y, bacular length was highly, positively correlated with age (y) (r = 0.825, n = 38; Fig. 3). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, strictly speaking bacular length could not be used as a reliable indicator of absolute age based on a simple linear model but could be used as a rough indicator of age.

For the range of ages available in this study (Table 2), the coefficient of variation in bacular length for young males 1-5 y (36.8%) was considerably higher than in older males (8-10 y, 6.6%; > 12 y, 10.7%).

Although bacular length was not a good indicator of absolute age, it was more accurately a 'rough indicator' of age group. When bacular length is known, the following linear discriminant functions can be used to categorise each observation into one of

Table 2 (LEFT). Summary statistics for bacular variables (1 - 9), according to age (y) and age group. Data presented as the mean ± SE, followed by coefficient of variation in round brackets, and bacular variable expressed as a percentage of bacular length. Maximum value of each variable (males of unknown-age) is also presented. All measurements are in mm, apart from bacular mass (g).

Variables: 1. Bacular length (BL); 2. Proximal height; 3. Proximal width; 4. Distal height; 5. Distal width; 6. Proximal shaft height; 7. Middle shaft height; 8. Distal shaft height; 9. Bacular mass. Number (n) is the number of bacula from individuals where their age had been determined based on dentition. Sample size given in square brackets where this does not equal total sample size. Mean value of variable ± SE for the 7 largest males (≥ 200 cm, SBL) of unknown-age; maximum value in brackets.

Table 3. Growth in mean bacular length (BL) relative to mean standard body length (SBL). Number (n) shows the number of canine aged animals where both BL and SBL were recorded. Of the 50 canine aged animals, SBL was not recorded for 12 animals, i.e. n = 38. Sample size is given in square brackets where this does not equal total sample size. Bacular length (BL) values are mean ± SE in mm. SBL is expressed as mean ± SE in cm. Relative bacular length (RBL) is defined as 100% x BL (mm)/SBL (mm).

Age group	Age (y)	n	Mean bacular length (BL) (mm)	Mean SBL (cm)	Relative Bacular Length (RBL) (RBL = 100xBL/SBL)
Pup	< 1	3	28.5 ± 1.6 [3]	69.0 ± 2.5 [3]	4.1% [3]
Yearling	1	5	47.8 ± 1.7 [5]	90.6 ± 2.7 [5]	5.3% [5]
Subadult	4	1	86.6	137.0	6.3%
	5	3	-	-	-
	6	2	102.2 (1 measured)	145.0 (1 measured)	7.0% [1]
	7	11	106.5 ± 3.0 [6]	159.8 ± 4.5 [6]	6.7% [6]
	4-7	**17**	**103.5 ± 3.3 [8]**	**155.1 ± 4.6 [8]**	**6.7% [8]**
Adult	8	8	110.0 ± 3.2 [7]	167.1 ± 7.1 [7]	6.6% [7]
	9	4	117.3 ± 3.8 [3]	171.0 ± 3.2 [3]	6.9% [3]
	10	3	117.8 ± 2.9	187.0 ± 1.7	6.3% [3]
	8-10	**15**	**113.5 ± 2.2[13]**	**172.6 ± 4.4 [13]**	**6.6% [13]**
	≥ 12	10	113.2 ± 4.3 [9]	185.9 ± 7.7 [9]	6.1% [9]
Total		**50**	**38**	**38**	**38**

four age groups (pups, yearlings, subadult, adults):

Pup = -5.50 + 0.39 x **BL**
Yearling = -15.53 + 0.65 x **BL**
Subadult = -67.25 + 1.35 x **BL**
Adult = -87.77 + 1.54 x **BL**

where, **BL** = bacular length (mm); Age Classes: pup, yearling, subadult and adult. The seal is classified into the age group associated with the linear discriminant function which results in the **minimum** value (see Stewardson et al., 2008, 2009). Of the 50 animals in this study, 86% were correctly classified using this method (Table 5).

Bacular length as an indicator of SBL

The plot of Log_e (**BL**) vs. Log_e (**SBL**) is shown in Fig. 4. Log_e Bacular length (**BL**) was highly positively linearly correlated with **SBL** (r = 0.877, n = 86; Fig. 4) on a plot of **SBL** (cm) vs. **BL** (mm) using robust Huber M Regression. When bacular length is known, the following equation (linear least squares fit; Log_e transformed data) can be used to predict Log_e (**BL**);

Log_e (**BL**) = -2.062 (± 0.247) + (1.3142 ± 0.0493) x Log_e (**SBL**)

where, the Spearman rank-order correlation was 0.877. M-estimate was not significant for bias (p = 0.0945) but LS-estimates for bias were significant (p = 0.00048).

Bivariate allometric regression

Spearman rank-order correlations show that bacular variables were significantly ($p \leq 0.01$) with

Table 4. Growth in bacular variables (1-9) relative to the mean value of bacular measurement (i) at age zero, RGR Y0 and (ii) from the previous year, RGR Yt-1. Growth in SBL is also given. All measurements are in mm, apart from the SBL (cm) and the bacular mass (g).

Variables: 1. Bacular length (BL), 2. Proximal height, 3. Proximal width, 4. Distal height, 5. Distal width, 6. Proximal shaft height, 7. Middle shaft height, 8. Distal shaft height, 9. Bacular mass. n is the number of canine-aged animals. SBLs of 12 animals were not recorded. Values for growth relative to age zero are presented on the left side of the relevant columns, i.e. [(Yt-Y0)/Y0] x 100 where Yt is the mean value at time t and Y0 is the value at time zero. Values for growth relative to the previous year are presented on the right hand side of the relevant columns. For animals 7 to 10 y of age, i.e. [(Yt-Yt-1)/Yt-1] x 100 where Yt-1 is the mean value for the previous year class and Yt is the mean value at time t. Sample sizes are given in brackets where this does not equal the total sample size. Instances where growth could not the calculated are marked (*) and there are two cases where the calculated growth is negative (adult age 7y; Var 4 and adult age 9y; Var 2).

Age Class	Age (y)	n	SBL	Var1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	-	-	-	-	-	-	-	-	-	-
Yearling	1	5	31	68	36	21	31	2	26	13	14	200
Subadult	4	1	99	204	106	89	227	68	149	150	128	2300
	5	3	*[0]	241	266	120	322	152	196	164	157	3300
	6	2	110 [1]	249	218	91	386	131	200	145	133	2950
	7	11	132; * [6]	256; 2.0	282; 20.4	118; 13.7	379; -1.5	143; 5.1	206; 2.0	186; 16.5	176; 18.8	3964; 33.2
Adult	8	8	142; 4.6 [7]	391; 9.9	341; 15.3	169; 23.4	448; 14.5	158; 6.3	239; 10.8	211; 8.9	191; 5.2	5600; 40.3
	9	4	148; 2.3 [3]	311; 4.9	304; -8.3	209; 14.9	453; 0.9	193; 13.4	243; 1.2	245; 10.9	225; 11.6	7125; 26.8
	10	3	171; 9.4	313; 0.8	447; 35.3	285; 24.7	491; 6.9	268; 25.8	346; 30.1	268; 6.6	234; 3.1	7533; 5.7
	≥ 12	10	169 [9]	297	343	189	495	196 [8]	320	290	241	8150
Total		**50**	**38**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**	**50**

each other (Table 6). Distal width (**Var 5**) with proximal width (**Var 3**) had the lowest correlation (r = 0.67) but most equal or exceed r = 0.80. Plots of all the data used for the bivariate allometric regressions can be found in Stewardson (2001). In the present study, the slope and intercept values and correlation coefficients (**r**) are shown in Tables 7, 8 and 9.

Regression of bacular measurement on SBL

Of the 103 seals in the study, 86 were used in regression analysis for the natural log of baculum measurement on Log_e (**SBL**). All pups (n = 3) were excluded from the regression analysis, and **SBL**s for 12 animals had not been recorded (see above).

There was little difference between the ordinary least square straight lines fitted to the data, and the 'robust' least squares straight lines fitted to the same data. The 'robust' straight line equations for regressing log of baculum measurement on log of seal length are given in Table 7. All bacular variables were highly, positively correlated with **SBL**, r ≥ 0.68. Relative to **SBL**, growth in distal height, distal width, proximal shaft height, distal shaft height and bacular mass was positively allometric; and proximal width was

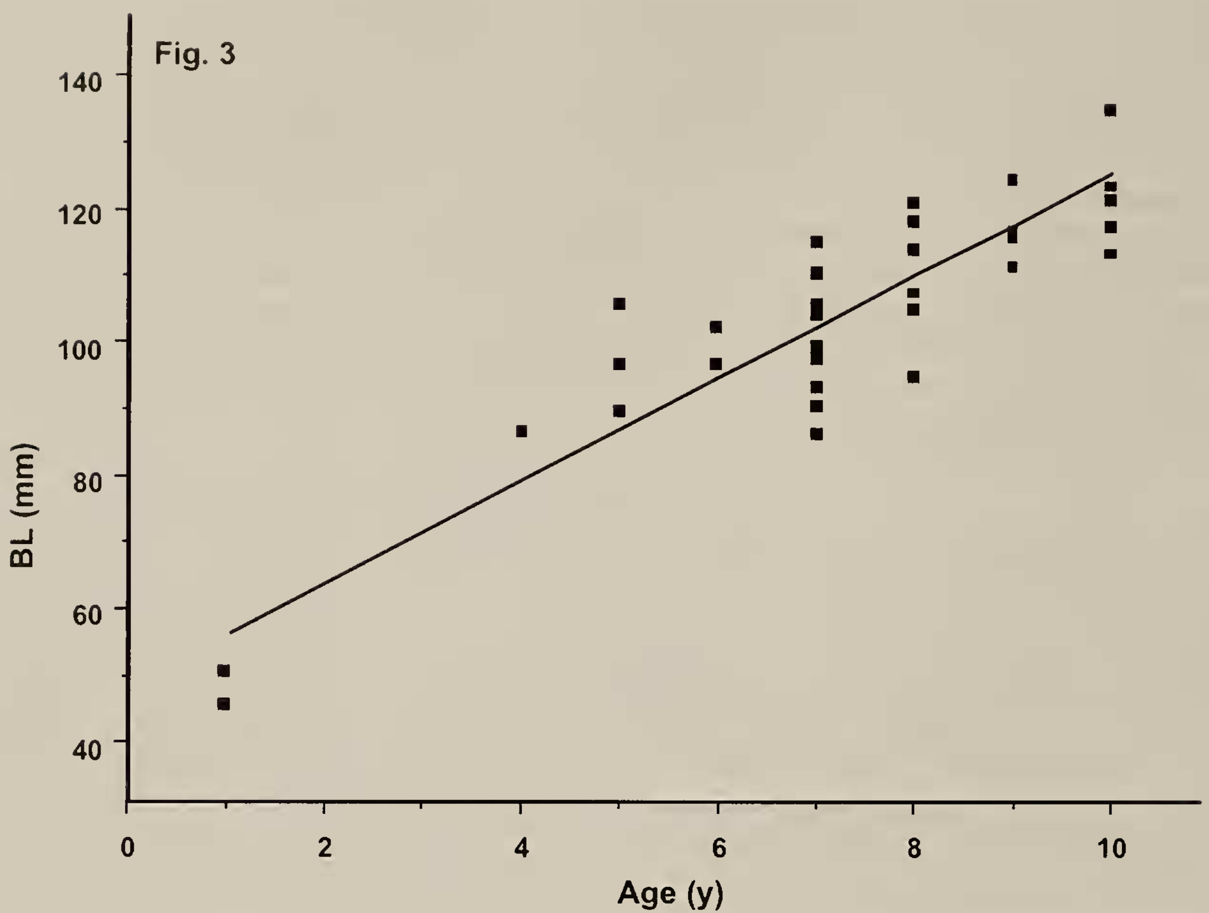

Fig. 3 Bivariate plot of Baculum Length (BL) (mm) vs. age (y) using Robust MM Linear regression. The fitted line was BL = 48.63 (± 10.39) + (7.678 ±1.346) x Age with a Spearman rank-order correlation of 0.825. The M-estimate and LS-estimate for bias were not significant. Robust MM Linear regression could also be run to predict Age (y) from BL. The fitted line was Age = -4.016 (± 1.166) + 0.108 (± 0.0111) x BL.

isometric (Table 7). Regression slopes for bacular length, proximal height and middle shaft height all had significant positive slopes > 1 (Table 7).

Value of bacular measurement on bacular length

Of the 103 seals in the study, 100 were used in regression analysis for natural log of baculum measurement on bacular length. All pups (n = 3) were excluded from the regression analysis.

All bacular variables were highly, positively correlated with bacular length, r ≥ 0.7 (Table 8). Relative to bacular length, growth in distal height, proximal shaft height and proximal height was positively allometric relative to bacular length; distal width and distal shaft height was isometric; and proximal width was negatively allometric (Table 8). Regression slopes for middle shaft height and bacular mass scaled with positive slope (Table 8). The slope for bacular mass was considerably steeper than for other variables.

Value of bacular measurement on age

Of the 40 seals aged from upper canines, 37 were used in regression analysis for the natural log of a baculum measurement versus age. As above, all pups (n = 3) were excluded from the regression analysis.

Overall, the plots of log bacular measurements versus log **SBL** were better described by linear relationships than the plots of $\log_e$ bacular measurements versus age (see Griffiths et al., 1998, p. 126). Fig. 3 shows a plot of **BL** vs. Age (y); data for this and other fits are shown in Table 9. Proximal height vs. Log_e **(SBL)** was the only variable that roughly resembled a straight line.

DISCUSSION

Bacular size

In South African fur seals (*Arctocephalus pusillus pusillus*) from the Eastern Cape coast, maximum

Table 5. Discriminant analysis for male seal age group (pup, yearling, subadult and adult) inferred from bacular length. Number (n) is the number of animals aged from counts of incremental lines observed in the dentine of upper canines, n = 50. Percentage of animals correctly classified into age group is given in brackets. Animal classified as adults includes animals ≥ 12 y.

Known Age Group	Classification into age group				
	n	Pup	Yearling	Subadult	Adult
		(age < 7 month)	(7 month < age < 18 month)	(18 month < age < 7 y 6 month)	(age ≥ 7y 6 month)
Pup	3	3 (100%)	0	0	0
Yearling	5	0	5 (100%)	0	0
Subadult	17	0	0	14 (82%)	4 (18%)
Adult	25	0	0	3 (16%)	21 (84%)
Total	**50**	**3**	**5**	**17**	**25**

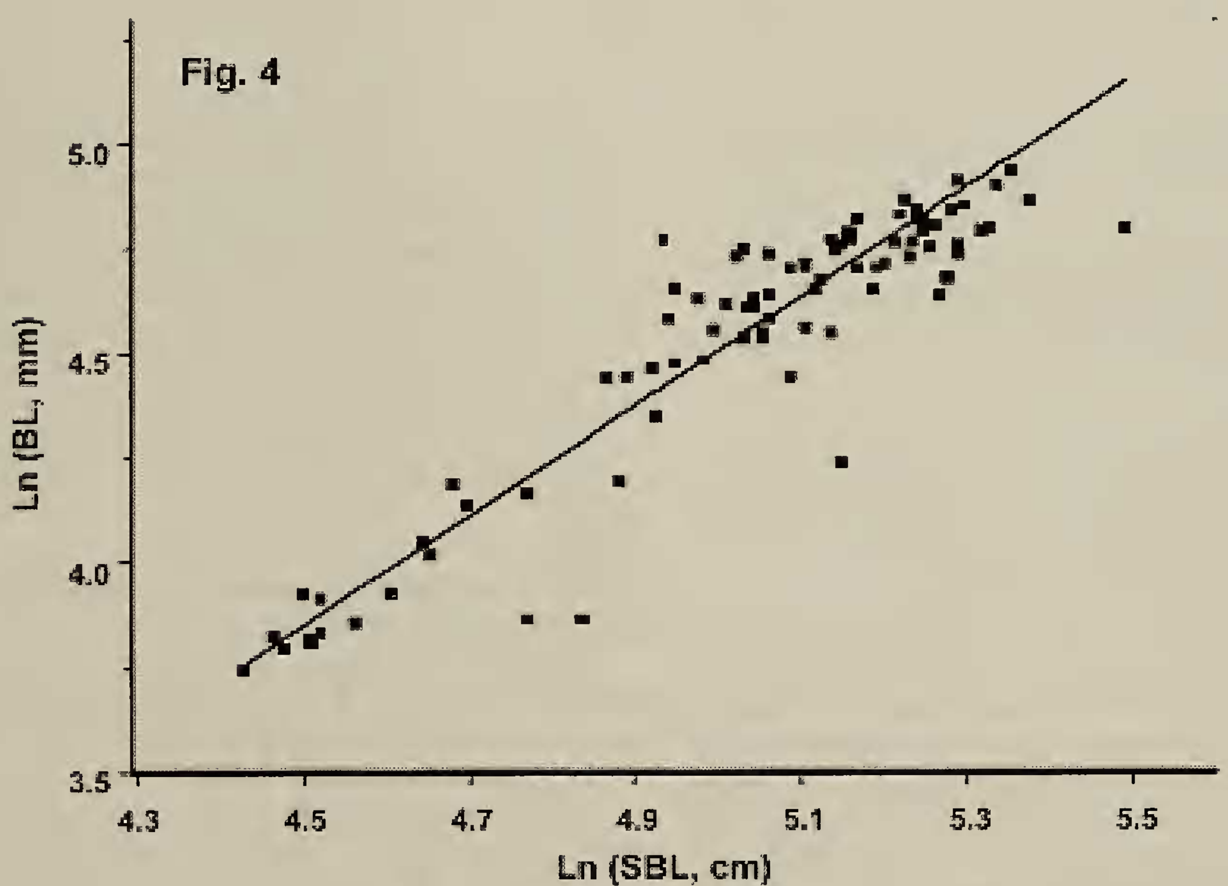

Fig. 4 Bivariate plot of Loge (BL) vs. Loge (SBL) using Robust MM Linear regression. The fitted line was Loge (BL) = -2.062 (± 0.247) + (1.3142 ± 0.0493) x Loge (SBL) with a Spearman rank-order correlation of 0.877. The M-estimate was not significant for bias (p = 0.0945) but the LS-estimate for bias was significant (p = 0.00048).

Table 6. Spearman rank-order correlation coefficients for log bacular variables. Variables: 1. bacular length (BL); 2. Proximal height; 3. Proximal width; 4. Distal height; 5. Distal width; 6. Proximal shaft height; 7. Middle shaft height; 8. Distal shaft height; 9, bacular mass. Two distal width measurements were not recorded because specimens PEM2049 and PEM2134 were damaged hence Var 5 has only 101 records. All correlations are significant at the 1% level (2-tailed), i.e. p < 0.01.

	Var 1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Var 1 (BL)	1.00	0.82	0.71	0.90	0.80	0.88	0.92	0.90	0.95
Var 2	0.82	1.00	0.80	0.76	0.75	0.85	0.84	0.80	0.85
Var 3	0.71	0.80	1.00	0.69	0.67	0.76	0.75	0.70	0.77
Var 4	0.90	0.76	0.69	1.00	0.80	0.86	0.89	0.88	0.92
Var 5	0.80	0.75	0.67	0.80	1.00	0.79	0.80	0.80	0.83
Var 6	0.88	0.85	0.76	0.86	0.79	1.00	0.94	0.89	0.94
Var 7	0.92	0.84	0.75	0.89	0.79	0.94	1.00	0.96	0.97
Var 8	0.90	0.80	0.70	0.88	0.80	0.89	0.96	1.00	0.95
Var 9	0.95	0.85	0.77	0.92	0.83	0.94	0.97	0.95	1.00
Total	**103**	**103**	**103**	**103**	**101***	**103**	**103**	**103**	**103**

bacular length we found in the present study was 139.3 mm and mass was 12.5 g; however bacula up to 141 mm (Oosthuizen and Miller, 2000) and 16.8 g (Rand, 1949) have been reported for South African fur seals from other areas. Baculum length was similar to that of the Northern fur seal (*Callorhinus ursinus*) (Scheffer, 1950) and the harp seal (*Pagophilus greonlandicus*) (Miller and Burton, 2001; Miller 2009), which is a phocid seal. As with other Otariidae, bacular length of the South African fur seal is considerably smaller (proportionately to standard body length, **SBL**) than that of most Phocidae and the Odobenidae (Scheffer and Kenyon, 1963; Miller and Burton, 2001).

No systematic quantitative study seems to have been made of the growth with age of the baculum of the Australian fur seal (*Arctocephalus pusillus doriferus*) or the New Zealand fur seal (*Arctocephalus forsteri*). Basic morphometric data on the bacula of Australian and New Zealand fur seals do not appear to be readily available (Scheffer and Kenyon, 1963). At present it would be very easy to pass off illegally obtained bacula from Australian and New Zealand seals as legal South African material.

Bacular shape

Although detailed information on the morphology of the otariid bacula is sparse, bacular shape was most similar to the Northern fur seal and California seal lion (Kim *etal.,* 1975; Morejohn, 1975; King, 1983). For example, in *Arctocephalus* fur seal species, Northern fur seal and California seal lion, the adult bacular apex consists of a dorsal and a ventral knob. When viewed anteriorly, the knobs are parallel sided (*Arctocephalus* species and the California sea lion), or resemble a figure-of-eight in the California sea lion. Apical keels (lateral expansion of the apex) are present on the baculum of some California sea lion individuals, yet absent in both *Arctocephalus* species and the Northern fur seal (Kim *et al.,* 1975; Morejohn, 1975).

Bacular length (BL) as an indicator of Standard Body Length (SBL) and age

As with other species of pinnipeds, there is considerable variation in **BL** with age, especially in younger animals (Rand, 1949; Scheffer, 1950; Bester, 1990; Oosthuizen and Miller, 2000).

In male South African fur seals, **BL** was found to be a 'rough indicator' of **SBL** and age group, but not of absolute age. The classification criteria for age group, and **SBL**, developed in this study will be particularly useful when teeth are not available for age determination; a seal is decomposed/scavenged (total **SBL** cannot be measured) or because the skull is incomplete/absent (total **SBL** cannot be extrapolated from skull length); or museum records have been misplaced or destroyed. As more specimens become

Table 7 `Robust' least squares straight line equations (y = mx + b), Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log seal body length (cm). The number (n) is for the total number of bacula from canine-aged animals and for animals of unknown-age (the 3 pups were excluded from analysis, and SBLs from 14 males were not recorded, i.e., n = 86 bacula). r is Spearman rank-order correlation coefficient. All correlations were significant at the 1% level (2-tailed), m is the determined slope of the fitted line. NA, tests not applicable because the model assumptions required to test hypotheses about the slope of the line (m) were not met. Not significant (ns) since the p-value was > 0.05, we cannot reject Ho, in favour of H1 at the 5% significance level; therefore growth is isometric. * For distal width (Var 5) n = 84 because distal width measurements could not be measured on two specimens (see Table 6).

Dependent variable	Linear regression					Allometry		
	n	Intercept (b) ± SE	Slope (m) ± SE	r	(p-values)	Alternative Hypothesis	df	p-value
1. Length of baculum (BL)	86	-1.67 ± 0.22	1.23 ± 0.04	0.88	(< 0.01)	NA	NA	NA
2. Proximal height	86	-5.58 ± 0.45	1.54 ± 0.09	0.78	(< 0.01)	NA	NA	NA
3. Proximal width	86	-3.12 ± 0.48	1.03 ± 0.09	0.68	(< 0.01)	H_1: m ≠ 1	84	0.78 ns
4. Distal height	86	-7.88 ± 0.46	2.00 ± 0.09	0.84	(< 0.01)	H_1: m > 1	84	< 0.01
5. Distal width	84*	-5.64 ± 0.04	1.38 ± 0.09	0.80	(< 0.01)	H_1: m > 1	82	< 0.01
6. Proximal shaft height	86	-5.59 ± 0.29	1.50 ± 0.06	0.87	(< 0.01)	H_1: m > 1	84	< 0.01
7. Middle shaft height	86	-5.92 ± 0.28	1.53 ± 0.06	0.90	(< 0.01)	NA	NA	NA
8. Distal shaft height	86	-5.24 ± 0.29	1.36 ± 0.06	0.87	(< 0.01)	H_1: m > 1	84	< 0.01
9. Mass of baculum	86	-21.51 ± 0.68	4.51 ± 0.13	0.91	(< 0.01)	H_1: m > 1	84	< 0.01

Table 8. 'Robust' least squares straight line equations ($y = mx + b$), Spearman rank-order correlation coefficients and allometry for loge (bacular measurement) on loge (bacular length). Number (n) is the total number of bacula for canine-aged animals and animals of unknown-age (the 3 pups were excluded from analysis, i.e., n = 100 bacula). * For distal width (Var 5) n = 98 because two specimens were damaged (see Table 6). r is the Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed). Test not applicable (NA) because model assumptions required to test hypotheses about the slope of the line (m) were not met. Not significant (ns) since the p-value was > 0.05, we cannot reject H_0 in favour of H_i at the 5% significance level; therefore growth is isometric.

D.pendent variable	Linear regression					Allometry		
	n	Intercept (b) ± SE	Slope (m) ± SE	r	(p-values)	Alternative Hypothesis	df	p-value
2. Proximal height	100	-3.11 ± 0.26	1.21 ± 0.06	0.80	(< 0.01)	H_i: m > 1	98	< 0.01
3. Proximal width	100	-1.52 ± 0.29	0.79 ± 0.06	0.69	(< 0.01)	H_i: m < 1	98	0.15 ns
4. Distal height	100	-5.07 ± 0.18	1.60 ± 0.04	0.89	(< 0.01)	H_i: m >1	98	< 0.01
5. Distal width	98*	-3.61 ± 0.26	1.08 ± 0.06	0.79	(< 0.01)	H_i: m ≠ 1	96	0.15 ns
6. Proximal shaft height	100	-3.30 ± 0.17	1.16 ± 0.04	0.87	(< 0.01)	H_i: m > 1	98	< 0.01
7. Middle shaft height	100	-3.52 ± 0.15	1.17 ± 0.03	0.91	(< 0.01)	NA	NA	NA
8. Distal shaft height	100	-3.18 ± 0.29	1.05 ± 0.04	0.89	(< 0.01)	H_i: m ≠ 1	98	0.15 ns
9. Mass of baculum	100	-14.66 ± 0.29	3.49 ± 0.06	0.94	(< 0.01)	NA	NA	NA

Table 9. 'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log (bacular measurement) vs. age (y) and for log (weight) vs. age (y). n is the total number of bacula for canine-aged animals (only animals 1 to 10 y were included in the analysis, hence n = 37). SBLs for 11 aged males were not recorded. r is the Spearman rank-order coefficient. All correlations were found to be significant at the $p < 0.01$ level (2 tailed).

Dependent variable	'Robust' Log-Linear regression			
	n	Intercept (b) ± SE	Slope (m) ± SE	r (p-values)
1. Length of baculum (**BL**)	37	3.88 ± 0.05	0.10 ± 0.01	0.83 (< 0.01)
2. Proximal height	37	1.13 ± 0.08	0.15 ± 0.01	0.67 (< 0.01)
3. Proximal width	37	1.31 ± 0.09	0.11 ± 0.01	0.78 (< 0.01)
4. Distal height	37	1.10 ± 0.10	0.17 ± 0.01	0.76 (< 0.01)
5. Distal width	37	0.45 ± 0.07	0.13 ± 0.01	0.68 (< 0.01)
6. Proximal shaft height	37	1.05 ± 0.06	0.13 ± 0.01	0.74 (< 0.01)
7. Middle shaft height	37	0.89 ± 0.13	0.13 ± 0.01	0.85 (< 0.01)
8. Distal shaft height	37	0.82 ± 0.06	0.11 ± 0.01	0.79 (< 0.01)
9. Mass of baculum	37	-1.28 ± 0.15	0.37 ± 0.02	0.87 (< 0.01)
Standard body length (**SBL**)	26	4.46 ± 0.04	0.08 ± 0.01	0.83 (< 0.01)

available, the classification criteria would be expected to become more precise. Statistics on age vs. bacular length show that bacular length can be used as a rough indicator of age (Fig. 3) and show that it is a better indicator of age than Standard Body Length (**SBL**) in terms of correlation coefficient (r) and error of the predicted age (Stewardson et al., 2009). More determinations of bacular length in tagged bulls of known age could prove it to be a very useful method.

Bacular growth

In male South African fur seals, growth of the baculum is a differential process with most variables growing rapidly relative to **SBL** and bacular length (**BL**). Two variables were isometric and one was negatively allometric, relative to bacular length, indicating that the adult baculum was not simply an enlarged version of the juvenile baculum (see Fig. 2).

Growth changes in **BL** and mass described in this study generally support findings reported by Oosthuizen and Miller (2000) and are also similar to those reported for the harp seal (Miller and Burton, 2001) which is a phocid seal. In this study, based primarily on animals collected from the south and south-west coast of southern Africa, growth in **BL** took place rapidly up until 5 y; peaked at 9-10 y; and then slowed. Our findings could not be compared to those of Rand (1956) because, in the latter, age was estimated from cranial suture closure which has subsequently been shown to be an unreliable indicator of absolute age in this species, particularly for animals ≥ 12 y (Stewardson et al., 2008).

The biological significance of bacular growth patterns

In male South African fur seals, a growth spurt in **BL** occurs at 2-3 y (Rand, 1949; Oosthuizen and Miller, 2000), when males attain puberty (Stewardson et al., 1998). Unfortunately, we have very scanty details on the life history of South African fur seals during the dispersive juvenile stages of their life. After puberty, the baculum continues to increase in length with increasing age, approximating full length at about 9 y (Oosthuizen and Miller, 2000; present study). Bacular dimensions, other than length, approximate full size between 8-10 y (present study), when most males have attained full reproductive capacity (Stewardson et al., 1998). Although males can sire offspring at a young age (e.g., at 4 y in captivity; Linda Clokie-Van Zyl, pers. comm.), bacular growth is geared to coincide with the attainment of social maturity, presumably to enhance the effectiveness of copulation.

Socially mature male South African fur seals: (i) may achieve a high level of polygyny at large colonies (David, 1987); (ii) usually copulate once with each harem female, 5-7 days postpartum during a brief breeding season (November to late December) (David and Rand, 1986); and (iii) usually exhibit brief intromission duration (Stewardson, pers. obs.). In such males, the baculum is therefore large enough to provide sufficient mechanical support for insertion and repeated copulations (with potentially numerous females within a short period of time), and may assist in deeper penetration. The ornate apex presumably serves to stimulate the vagina of the female (Eberhard, 1985, 1996). However, the function of the apex in this species remains unclear considering that: (i) female South African fur seals are not 'induced ovulaters' like cats; (ii) copulation occurs when the female is sexually receptive and (iii) sperm competition is weak (Stewardson et al., 1998).

CONCLUSION

Data presented in this study provide more detailed information on the morphology of the South African fur seal bacula than earlier descriptions given by Rand (1956) and Mohr (1963), based on smaller data sets and more dubious age estimates. Oosthuizen and Miller (2000) used a larger data set than the present study but did not attempt a detailed analysis of bacular morphometrics. Our study provides new information on the patterns of bacular growth in relation to age and **SBL** (Oosthuizen and Miller, 2000), and demonstrate that bacular length is a 'rough indicator' of **SBL** and age group. Similar overall conclusions have been drawn from analysis of larger data sets available for the harp seal (Miller et al., 1998, 1999; Miller and Burton, 2001) which is a member of the phocidae (or true seals). The seal baculum is a heterotopic bone and so it is likely that it shows at least some growth throughout life. We have found that the size of the baculum relative to SBL does decrease in old bulls but perhaps growth layer groups (GLG) can be determined by histological sectioning of bacula. It might provide a means to estimate age in very old individuals where dentition no longer gives useful estimates of age. Bacular measurements on very old bulls where the age is known from tagging or from zoo animals are needed.

Further studies examining the morphology and growth patterns of the pinniped bacula from known age animals are required to establish species affinities and develop identification protocols for seal bacula.

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